VARIATION IN NEST SITES, NESTING SUCCESS, TERRITORY SIZE, AND FREQUENCY OF POLYGYNY IN WINTER WRENS IN NORTHERN TEMPERATE CONIFEROUS FORESTS

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ABSTRACT.—We studied the nesting ecology of Winter Wrens (*Troglodytes troglodytes*) from 1994–1996 in coastal, coniferous, temperate rain forest of southeastern Alaska. Overall nesting success (estimated by the Mayfield method) of 143 nests exceeded that reported for other published studies of temperate wrens, including *T. troglodytes*. Wrens used understory nest sites (logs, stumps, root disks of uprooted trees, understory moss, stream banks) in two forest sites where predation of nests was low (2% of 65 nests). Males at these two sites commonly had small territories (1.8 ha ± 0.3 SE and 1.2 ha ± 0.1 SE) and often mated polygynously (22% and 78% of males had at least two mates). In the third study area, where predation (probably by red squirrels, *Tamiasciurus hudsonicus*) on understory nests was relatively high (19% of 59 nests), nests most often were placed in moss clumps on tree branches, as high as 18 m above ground. Males in this study area had the largest territories (2.8 ha ± 0.4 SE) and most (90%) mated monogamously. Variation in nesting ecology among these three superficially similar (mature conifer forest) sites may be related to subtle differences in habitat features and predator abundance. *Received 12 September 2001, accepted 3 June 2002.*

The Winter Wren (*Troglodytes troglodytes*), an insectivorous understory passerine, occurs over a large geographical range, including both Eurasia and North America (Hejl et al. 2002). The ecology of this bird has been well studied in Europe, but has received much less attention in North America (Armstrong 1992, Hejl et al. 2002). Even though the Winter Wren is one of the most common birds in northern temperate coniferous forests of southeastern Alaska and coastal British Columbia (Arnott et al. 1995, Willson and Comet 1996), descriptions of its habitat use have been few (Heath 1920, McLachlin 1983, Waterhouse 1998, Van Horne and Bader 1990), descriptions of its nesting ecology have been limited to nest site selection (Waterhouse 1998), and no studies have documented nesting success.

We describe and compare nest placement, nesting success, territory size, and frequency of polygyny of Winter Wrens in several co-niferous forest sites in southeastern Alaska and relate differences among populations, *a posteriori*, to differences among habitat features at these sites.

METHODS

Study area.—We conducted our study of Winter Wren nesting ecology during May through July, 1994–1996, in coastal, coniferous, temperate rain forest of southeastern Alaska. Our three primary study sites (45–60 ha), Peterson Creek and Fish Creek on Douglas Island, and Herbert River on the mainland, were located near the city of Juneau (58° 22′ N, 134° 35′ W). During the course of other field studies, we also recorded some wren nests at ancillary sites on the mainland near Juneau (Montana Creek, one nest; Sheep Creek, 14 nests), on Catherine and Baranof islands near Hanus Bay (57° 24′ N, 135° 00′ W; three nests), and on Kupreanof Island near Portage Bay (57° 00′ N, 133° 12′ W; two nests). Data from ancillary sites were used in general descriptions of nest site placement and in overall assessment of nesting success, but no comparisons were made with the three primary sites. The overstory vegetation of all sites except Sheep Creek was dominated by coniferous tree species, primarily western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*), with some mountain hemlock (*T. mertensiana*) and yellow-cedar

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(*Chamaecyparis nootkatensis*), the latter especially on Baranof, Catherine, and Kupreanof islands. Tree species composition and forest structure differed among sites because of anthropogenic (logging) and natural forces (postglacial sediment deposition on alluvial floodplain). The Fish Creek and Peterson Creek sites were mature, uneven-aged spruce-hemlock forests from which selective logging approximately 80–90 years ago removed many dominant spruce (T. Pence pers. comm.). The terrain at Fish Creek was more rugged, characterized by rocky cliffs along the stream, and the forest had a more open understory than Peterson Creek. The Herbert River site was an even-aged, mature spruce forest on flat terrain between two glacial rivers (Herbert and Eagle rivers). Some selective tree harvest for construction of a mining road occurred about 50 years ago (T. Pence pers. comm.). The forest at Herbert River was dominated by mature spruce, with scattered black cottonwood (*Populus trichocarpa*), and some suppressed western hemlock in the understory. Red alder (*Alnus rubra*) was present along the streams at all three sites. Ancillary sites included low elevation mature coniferous forest, some selectively logged 30–80 years ago (R. Deal pers. comm.), uncut mature coniferous forests on moderate to steep slopes with small streams, and a deciduous valley with small coniferous forest patches (see Willson and Comet 1996 for description). The understory vegetation used by wrens for nest cover or foraging in coniferous forest sites generally consisted of yellow skunk cabbage (*Lysichiton americanum*), blueberry (*Vaccinium* spp.), devil's club (*Oplopanax horridum*), salmonberry (*Rubus spectabilis*), currants (*Ribes* spp.), elderberry (*Sambucus racemosa*), rusty menziesia (*Menziesia ferruginea*), and a variety of mosses (see Alaback 1982).

We measured the relative abundance of potential nest sites within most nesting territories (see territory sizes, below) during 1996 by counting the number of potential nest sites (i.e., understory wood: logs, stumps, and root disks of uprooted trees; understory moss: moss skirts at the bases of tree trunks and moss-covered mounds on the ground; and arboreal moss: clumps of moss hanging from tree branches) in 20 5-m radius plots selected arbitrarily throughout each territory. We also measured the length of stream bank suitable for nesting within each territory. We judged potential nest sites based on the kinds of sites used for nests during previous years. We also used these data to derive a general description of the habitat at each of the three main study sites. During 1998, we determined the species and dbh of all trees taller than 1.3 m along four 200-m transects (nine 5-m radius plots per transect; 2,826 m² sampled per site) positioned ≥200 m apart at the three main study sites.

Nest monitoring.—Our nest-searching effort varied among years. During 1994, while conducting another study we documented wren nests at two of the three main study sites (Peterson Creek and Herbert River). We focused on wren nesting ecology at Fish Creek and Herbert River during 1995 and at Herbert River, Peterson Creek, and Fish Creek during 1996. Nest searches began at first light (approximately 03:00 AST) and continued until approximately 12:00. During each year, 6–10 observers searched for nests on 40–60 days.

Most nests (85% of 143 with known outcome) were accessible and we checked their contents every 1–3 days; we determined the status of inaccessible nests (*n* = 21) by observing nesting behaviors of adults. We considered a nest to be (1) active if adults were observed tending eggs or young, (2) depredated if the nest showed obvious signs of depredation (eggshell fragments or torn nesting material), (3) failed due to weather if the nest showed obvious signs of disturbance from rain or flooding, (4) abandoned if the nest was not tended and cause of failure was unknown, or (5) successful if adults were observed feeding at least one young of known (for nests with known hatch dates) or estimated (based on appearance of young) fledging age (in this study: 16.0 days ± 0.6 SE, *n* = 12). We located fledglings within territories within 2 days after fledging to verify that fledging had occurred. We excluded from analyses nests abandoned during nest building and those not used for reproduction.

We used the Mayfield method (Mayfield 1975) with modifications of Hensler and Nichols (1981) to calculate nesting success, excluding seven nests with unknown outcomes. We used mean values for clutch sizes (5.6 eggs ± 0.2 SE, *n* = 11), incubation pe-

riods for complete clutches (16.0 days ± 0.9 SE, $n = 4$), and nestling periods (16.0 days ± 0.6 SE, $n = 12$) to determine observation days during each period of the nesting cycle. For calculations of percent nesting success, we included a 21-day period for egg laying and incubation (assuming incubation begins on the day of clutch completion), and a 16-day nestling period. Unless otherwise stated, all values of nesting success are estimates using the modified Mayfield calculation.

After a nest failed or the young fledged, we measured nest height above ground and (during 1995 and 1996 only) the percentage of vegetative cover around the nest. We determined lateral vegetative cover by using a clear plastic board divided into 25 1-cm squares. The nest was placed centrally within the grid held 1 m from the nest and 1 m in front of the observer's face. From each of the four cardinal directions, we determined the amount of vegetation obscuring the nest by counting the number of squares that were >50% filled by vegetation in front of the nest. We used the mean percent cover at the four cardinal directions to represent overall nest cover. We also measured nests with unknown outcomes and included the data in general descriptions of nest site use. Some nest measurements could not be obtained because nests were inaccessible to us or were still active during the last nest visit.

Territory sizes and pairing status.—During 1996, using mist nets and a tape recording of another male's territorial song, we captured and banded adult wrens (16 males and four females) to allow for identification of nest and territory ownership and pairing status (i.e., monogamous or polygynous). Individuals were banded with a USFWS aluminum band and a unique combination of plastic colored leg bands (Avinet, Dryden, New York). Once a nest was located, we began to delineate that male's territory by spot mapping singing males, territorial disputes, foraging activity, and interactions with females. We next located the nest(s) and determined the territory boundaries of the neighboring male wren. Multiple observers then simultaneously followed neighboring males for at least a 2-h period on each of five days to clarify boundaries. We also documented territory boundaries and pairing status for 11 unbanded males. Most

male wrens (24 of 27) had neighbors, and territories of unbanded males always were adjacent to banded males; using adjoining territories of males with active nests allowed us to better define territory boundaries (see Bibby et al. 1992).

The size of one territory was not estimated because the boundaries of his neighbors' territories were unknown. Males with multiple, concurrently active nests and males that tended fledglings and nestlings simultaneously were considered polygynous. Because few females were banded, we were unable to document sequential polygyny. Thus, for the purposes of this study, polygyny refers only to simultaneous polygyny.

To determine nest site selection, we tested for differences between distributions of nest site use and potential nest site availability within sites with log likelihood G-tests (Sokal and Rohlf 1995) for each of the primary study sites. If a significant difference was obtained, we constructed a 95% confidence interval for proportions of used sites and compared it to proportions of available sites to determine if nest sites were favored, avoided, or used in proportion to availability (Byers et al. 1984). We used the computer program CONTRAST, which uses a chi-square analysis with multiple comparisons (Hines and Sauer 1989) to analyze Mayfield daily survival rates. We used stepwise regression analysis with an entry criterion of 0.15 (SAS Institute, Inc. 2000) to examine relationships between territory sizes and availability of potential nest sites. We angular transformed all percentage data prior to analysis with parametric statistics and used a square root transformation on the potential nest site availability data because group variances were proportional to means (Zar 1999). For multiple comparisons, we used an adjusted alpha value to control for experimentwise error (Zar 1999).

RESULTS

Habitat features of main study sites.—Density of all tree species combined did not differ significantly among study sites, but the forest at Herbert River was characterized by more spruce and less hemlock of all size classes than the forests at Peterson Creek or Fish Creek (Table 1). Overall, Peterson Creek had the most downed wood in the understory (Ta-

TABLE 1. The density of trees did not differ significantly among the three main study sites in southeastern Alaska, 1998, but the Herbert River site was characterized by more spruce and less hemlock of all size classes than the other two sites. Values are mean ± SE number of trees per ha.

	Fish Creek	Herbert River	Peterson Creek	F	P
Sitka spruce	136 ± 66[a]	611 ± 79[b]	321 ± 73[a]	10.98	0.004
Western hemlock	650 ± 123[b]	107 ± 60[a]	611 ± 147[b]	6.82	0.016
Black cottonwood and red alder	0 ± 0	19 ± 7	7 ± 4	3.80	0.064
All tree species	926 ± 74	850 ± 96	1093 ± 17	1.10	0.375

[a,b] Means within a row with different superscripts are significantly different (ANOVA with Tukey's pairwise test; SAS Institute, Inc. 2000).

ble 2), where large decaying stumps and logs were common. There were fewer uprooted trees in the understory at Herbert River than at Fish Creek or Peterson Creek. The Herbert River site had the greatest abundance of thick mats of moss hanging from tree branches but the least amount of moss on the ground or on the bases of tree trunks. The Peterson Creek site provided much suitable stream bank whereas Herbert River provided very little.

Nest site selection and nesting success.— Most wren nests (143 of 150) were placed within cavities. Cavities most often were formed in moss growing on tree branches (54 nests), tree trunks (10 nests), decaying wood (7 nests), or on banks, cliffs, or the ground (12 nests). Wrens also used cavities in decaying logs, snags, and stumps (30 nests), live trees (five nests), and earthen banks (25 nests). Seven nests were built outside of a cavity, placed on tree branches or directly on the ground beneath logs or shrubs.

The distribution of nest site placement differed significantly (all $P < 0.005$) from po-

tential nest site availability at all study sites (all df = 3; Herbert River: $G = 27.7$; Fish Creek: $G = 55.1$; Peterson Creek: $G = 48.2$; Fig. 1). Most nests at Herbert River were in moss clumps on tree branches, proportional to availability, and bank nest sites, although rare, were favored. Most nests at Fish Creek were in understory wood and understory moss, in proportion to availability; moss clumps on branches, although fairly abundant, rarely were used. Most nests at Peterson Creek were in stream banks, although this type of site was relatively less abundant than moss clumps on tree branches.

Only at Herbert River did wrens consistently place nests ≥2 m above ground (mean nest heights: 6.9 m ± 0.8 SE, $n = 59$ at Herbert River; 1.1 m ± 0.1 SE, $n = 24$ at Fish Creek; 2.2 m ± 0.7 SE, $n = 43$ at Peterson Creek), despite availability of alternative nest sites in the understory (Table 2). The difference in nest height among sites was significant (ANOVA: $F_{2,124} = 18.48$, $P = 0.0001$; and Tukey's pairwise test, $P < 0.05$).

TABLE 2. Availability of potential nest sites for Winter Wrens differed among the three main study sites, southeastern Alaska, 1996. Values (except bank) are mean (± SE) relative abundances of all plots sampled within a site and are represented as mean number per m² of habitat. Values for bank are means of territories within sites and are expressed as m of bank per ha of territory.

Potential nest site	Herbert River	Fish Creek	Peterson Creek
Understory wood	2.3 ± 0.2[a]	2.1 ± 0.2[a]	4.4 ± 0.2[b]
Log	1.1 ± 0.1[a]	1.2 ± 1.1[a]	1.9 ± 0.2[b]
Stump	1.0 ± 0.1[b]	0.6 ± 0.1[a]	2.0 ± 0.1[c]
Root disk of uprooted tree	0.2 ± 0.04[a]	0.4 ± 0.1[b]	0.5 ± 0.1[b]
Arboreal moss (no. mossy branches)	15.4 ± 1.3[c]	3.9 ± 0.6[a]	8.2 ± 1.0[b]
Understory moss (mossy trunk bases, mossy ground mounds)	2.1 ± 0.1[a]	3.3 ± 0.2[b]	5.5 ± 0.3[c]
Earthen bank	7.2 ± 3.6[a]	47.8 ± 10.9[a]	398.0 ± 44.4[b]
No. plots (territories) sampled	160 (8)	200 (10)	160 (8)

[a,b,c] Means within a row with different superscripts are significantly different (ANOVA and Tukey's pairwise test; SAS Institute, Inc. 2000).
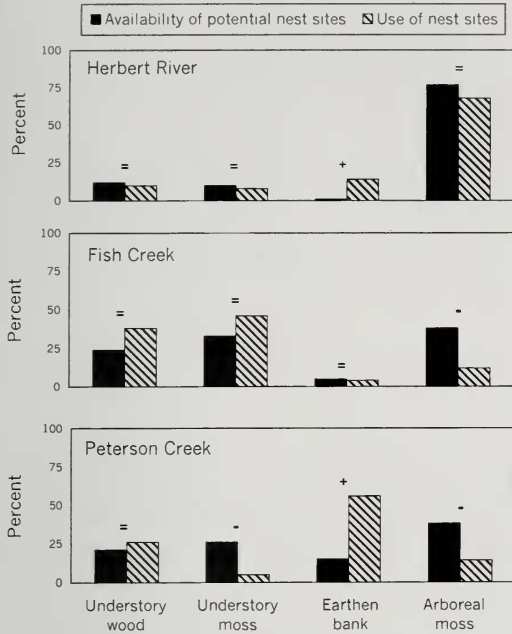
FIG. 1. Nest-site availability differed significantly from nest-site use (by G-test and simultaneous confidence intervals as described in Byers et al. 1984) by Winter Wrens at the three main study sites, southeastern Alaska, 1994–1996. Symbols indicate whether nest site type was selected (+), avoided (−), or used in proportion to availability (=). Sample sizes are 59 nests at Herbert River, 24 at Fish Creek, and 42 at Peterson Creek.

Only 19 (13%) nests with known outcome ($n = 143$) failed, and 12 of these failures were due to predation (Table 3). Daily mortality due to predation differed significantly among sites ($\chi^2 = 17.0$, df = 2, $P = 0.0002$) with highest mortality at Herbert River, where 11 (92%) predation events occurred (Herbert River versus Fish Creek: $\chi^2 = 16.0$, df = 1, $P = 0.0004$; Herbert River versus Peterson Creek: $\chi^2 = 9.80$, df = 1, $P = 0.0034$; Fish Creek versus Peterson Creek: $\chi^2 = 1.0$, df = 1, $P = 0.62$). Only three nests failed because of weather (i.e., flooding) and all were at Peterson Creek, where nests often were placed in the bank directly above the stream. The cause of the remaining five failures was unknown.

There was no significant difference in daily nest survival among years ($\chi^2 = 0.52$, df = 2, $P = 0.77$). Therefore, subsequent analyses were pooled over years. Nest predation was similar during the incubation (daily mortality: $0.007\% \pm 0.003$ SE) and nestling stages ($0.003\% \pm 0.001$ SE; $\chi^2 = 1.60$, df = 1, $P = 0.21$; within-site tests were not conducted because all but two predation events occurred at Herbert River).

In general, successful nests were higher above ground (4.4 m $\pm$ 0.5 SE, $n = 124$) than depredated ones (2.2 m $\pm$ 0.8 SE, $n = 13$; $t = 2.33$, df = 135, $P = 0.029$), but there was no significant difference in density of foliage surrounding nests (percent vegetative cover

TABLE 3. Winter Wren nesting success (by modified Mayfield estimate) was high in general, but predation did account for some nest failure, particularly at one of the three main study sites, southeastern Alaska, 1994–1996.

	Herbert River	Fish Creek	Peterson Creek	Ancillary sites	All nests, all sites
Number of nests (n)					
with known outcome	59	24	41	19	143
successful	47	22	37	18	124
failed	1	2	3	1	7
depredated	11	0	1	0	12
Observation days (n)					
incubation period	564	131	275	78	1,048
nestling period	759	307	481	188	1,735
Daily nest survival (mean $\pm$ SE)					
From predators	0.992 $\pm$ 0.002	1 $\pm$ 0	0.999 $\pm$ 0.001	1 $\pm$ 0	0.995 $\pm$ 0.001
All causes of failure	0.991 $\pm$ 0.003	0.995 $\pm$ 0.003	0.995 $\pm$ 0.003	0.996 $\pm$ 0.004	0.993 $\pm$ 0.002
Overall percent					
nesting success	69.2	80.8	76.8	76.3	72.9

TABLE 4. Monogamous and polygynous Winter Wrens experienced similar nesting success at the three main study sites, southeastern Alaska, 1996. There were no significant differences between daily nest survival of monogamous and polygynous pairings of banded birds ($\chi^2 = 0.08$, df $= 1$, $P = 0.78$) or pooled data including both banded and unbanded males ($\chi^2 = 0.12$, df $= 1$, $P = 0.73$).

	Number of successful nests (total nests)	Mayfield daily nest survival (observation days)
Monogamous pairings		
All males	15 (18)	0.992 ± 0.005 (308)
Only banded males	9 (11)	0.992 ± 0.005 (260)
Polygynous pairings		
All males	28 (31)	0.994 ± 0.003 (522)
Only banded males	17 (19)	0.994 ± 0.005 (309)

index; successful: 47.1% ± 4.0 SE, $n = 89$; depredated: 53.9% ± 11.9 SE, $n = 8$; $t = 0.72$, df $= 95$, $P = 0.47$). At Herbert River, where most of the predation events occurred, successful nests were significantly higher above ground (8.3 m ± 0.9 SE, $n = 47$) than depredated ones (2.4 m ± 0.9 SE, $n = 11$; $t = 4.51$, df $= 56$, $P = 0.001$) but had lower percent cover (19.9% ± 6.4 SE, $n = 30$ versus 50.7% ± 34.6 SE, $n = 7$, respectively; $t = 2.22$, df $= 35$, $P = 0.031$). Of the 11 predation events at Herbert River, 67% occurred at nests positioned in the understory (≤ 2 m of the ground); most nests were located much higher than 2 m (56% of nests were above 5 m). Nests in understory wood, understory moss, and banks at Herbert River were relatively more vulnerable to predators; over 30% of these types of nests were lost to predators versus only 8% of arboreal moss nests. In contrast, at Peterson Creek and Fish Creek, understory nests were common (over 80% of 67 nests), yet few (3%) were depredated.

Pairing status, territory size, and nesting success.—Overall during 1996, 37% of 27 male wrens were polygynous. Pairing status differed significantly among sites ($G = 13.53$, df $= 2$, $P = 0.001$). Most wrens at Herbert River (9 of 10) and Fish Creek (7 of 9) were monogamous, and all but one male at Peterson Creek ($n = 8$) had at least two females nesting on their territories. We noted one instance of trigamy at Peterson Creek and found no bachelors holding territories.

Territory sizes of males ($n = 26$) ranged from 0.7–4.8 ha (mean $= 2.0$ ha ± 0.2 SE). Mean territory size differed significantly among sites (2.8 ha ± 0.4 SE at Herbert River,

1.8 ha ± 0.3 SE at Fish Creek, 1.2 ha ± 0.1 SE at Peterson Creek; $F_{2,23} = 7.3$, $P = 0.004$); mean territory size at Herbert River was significantly larger than that at Peterson Creek or Fish Creek (Tukey's pairwise test, $P < 0.05$).

Polygynous males had significantly smaller territories (1.5 ha ± 0.2 SE, $n = 10$) than monogamous males (2.3 ha ± 0.3 SE, $n = 16$; $t = 2.2$, df $= 24$, $P = 0.038$). This relationship was largely a site effect, because most of the monogamous males were at Herbert River and most of the polygynous males were at Peterson Creek. There were too few polygynous males at Fish Creek and Herbert River, and too few monogamous males at Peterson Creek, to make within-site comparisons of territory sizes and pairing status. Monogamous and polygynous males experienced similar levels of nesting success (Table 4).

The stepwise regression analysis with territory size as the dependent variable entered only one independent variable, stream bank, into the model (parameter estimate $= 0.003$, SE $= 0.001$, $\chi^2 = 6.40$, $P = 0.011$). Territory size was inversely associated with this habitat feature.

DISCUSSION

In our study, nesting success was high (Mayfield estimated success of 73%; by simple percent, 87% of 143 nests fledged young), and exceeded that of all published studies of other northern Temperate Zone wrens: Bewick's Wren (*Thryomanes bewickii*; Kennedy and White 1996), Cactus Wren (*Campylorhynchus brunneicapillus*; Austin 1974), Carolina Wren (*Thryothorus ludovicianus*; Haggerty and Morton 1995), House Wren (*Trog-*

lodytes aedon; Li and Martin 1991, Johnson et al. 1993, Johnson and Kermott 1994), and Marsh Wren (*Cistothorus palustris*; Verner 1965, Leonard and Picman 1987). Furthermore, the nesting success we observed in southeastern Alaska exceeded that of this species in Europe (Garson 1980, Wesołowski 1983) and Idaho (Hejl et al. 2002). Predation was the most often mentioned cause of nest failure in all of these studies. In our study, nests in the nestling stage were not more vulnerable to predation than those in the incubation stage. Thus, chick begging apparently did not increase the risk of nest detection by predators, a result reported for other passerines as well (Cresswell 1997).

Despite high rates of nesting success in our study, predation was still an important risk, but only at the Herbert River site. Nearly all nests we found were placed in the understory except for those at Herbert River, where predation was relatively high. Most wrens at Herbert River nested in moss hanging from tree branches, and did so successfully. At Herbert River, nests near the ground were much more vulnerable to nest predators. A positive relationship between nesting success and height above ground has been found for other passerines as well (e.g., Li and Martin 1991). We also found that successful nests at Herbert River had less cover than unsuccessful ones, a result previously reported for the House Wren (Belles-Isles and Picman 1986, Li and Martin 1991). At the Herbert River site, nest cover and nest height probably were inversely related because nests built in moss hanging from tree branches were above the understory vegetation and, consequently, had little foliage cover. For wrens in our study, nest placement low to the ground was probably more influential than foliage cover in determining nest vulnerability.

The most probable nest predator at the Herbert River site was the red squirrel (*Tamiasciurus hudsonicus*; Sieving and Willson 1998). Squirrels harvest both hemlock and spruce cones but prefer the latter (O'Clair et al. 1997), which provide larger and more seeds (Pojar and Mackinnon 1994). Squirrels are far more abundant in spruce-dominated forests such as Herbert River than hemlock-dominated forests such as Fish Creek (TLD and MFW unpubl. data). Arboreal moss nests

at Herbert River probably afforded more protection from squirrels than nest sites nearer the ground. Squirrels spend much time on the ground collecting, eating, and caching cones and are likely to encounter a nest placed in the understory. Squirrels also forage for cones in trees, but cones are produced primarily on upper branches (Burns and Honkala 1990), and wren nests are located on lower branches. A squirrel actively searching for nests probably would be less likely to discover an arboreal moss nest because of the overwhelming abundance of such nest sites at Herbert River scattered throughout a strongly three-dimensional environment. We postulate that by nesting in a type of site that was overwhelmingly abundant, diffusely distributed, and positioned out of the regular path of squirrels, arboreally nesting wrens decrease the likelihood of being discovered by this predator.

Territory sizes differed among the three main study sites. Other studies have reported territory sizes for *T. troglodytes* ranging up to 42 ha (Zimin 1972, Glue 1973, Lea and Bourne 1975, Hejl et al. 2002), with the smallest territories (<2.5 ha) associated with wet, wooded habitats (Armstrong and Whitehouse 1977, Steiof 1991), forests with an abundance of dead wood in the understory (Batten 1976; Wesołowski 1981, 1983; McLachlin 1983), and areas of high insect abundance (Cody and Cody 1972). We found territory size to be related to only one measured feature, stream bank, which was identified as an important element of nesting habitat.

The level of polygyny differed among study sites, with the level at one site, Peterson Creek, being much higher than other published reports (Armstrong and Whitehouse 1977, McLachlin 1983, Wesołowski 1987, Hejl et al. 2002). Polygyny is predicted to be more prevalent in areas where resources, such as food or nest sites, are abundant and unevenly distributed (Emlen and Oring 1977). The clumped distribution of stream bank nest sites at our study site with the highest polygyny may have facilitated resource monopolization and a high frequency of polygyny by male wrens at that site. Nest sites on moss-covered tree branches were abundant at Herbert River, but these sites, due to their uniform distribution across the habitat, probably were difficult to monopolize.

In some instances, females may select already mated males at least in part because they gain access to higher quality nest sites, as reported for House Wrens (Johnson and Searcy 1993). In our study, since some concurrently active nests within the same territory were as close as 30 m, it is unlikely that secondary females settled with already mated males because they were unable to discern the mating status of males prior to nesting.

The nesting ecology of Winter Wrens in southeastern Alaska appears to differ from that elsewhere, at least in terms of nesting success, nest site use, and level of polygyny. Furthermore, within southeastern Alaska, several aspects of nesting biology and measures of reproductive fitness differed in habitats that were superficially similar (mature coniferous forest). Wrens also nest in habitats in southeastern Alaska that are structurally very different from mature coniferous forest, such as clearcuts, regenerating second growth, and deciduous forest patches (Van Horne 1984, Kessler and Kogut 1985), where nesting ecology may differ from that in mature conifer forests. Studies of *T. troglodytes* in Europe also suggest that the reproductive ecology of this bird varies among populations in various habitats in a number of measurable ways (nesting success, territory size, pairing status; Wesołowski 1981, 1983, 1987; Armstrong 1992). Wrens nesting in deciduous forests in Poland had greater pairing success and smaller territory sizes than those nesting in coniferous forests (Wesołowski 1983), and territory size was inversely related to invertebrate prey abundance in Britain (Cody and Cody 1972). Clearly, it is necessary to examine a wide range of habitats to understand habitat relationships of Winter Wrens and it is not possible to extrapolate accurately from one or a few studies. The information presented here also suggests that altering the understory and forest structure may affect not only the density but also the reproductive ecology of this understory bird.

ACKNOWLEDGMENTS

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